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STUDIES ON THE CIRRIPEDIA ACROTHORACICA
III. DEVELOPMENT OF THE FEMALE AND MALE OF *BERNDTIA PURPUREA* UTINOMI[1]

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With 15 Text-figures and 2 Tables

CONTENTS

Introduction

This is a continuation of my "Studies on the Cirripedia Acrothoracica" and represents the last part of the accounts on *Berndtia purpurea* UTINOMI. In the first part of this series the ecology and external morphology of the female were treated (UTINOMI, 1957) and in the second part the internal anatomy of the female was described in detail (UTINOMI, 1960). Here in this third part the larval development of both the female and male, and the morphology of the adult male will be given.

Very little is known of the development of the Acrothoracica, except for that of *Trypetesa lampas* (HANCOCK), which was first described by HANCOCK (1849) and DARWIN (1854) rather briefly and later studied by KÜHNERT (1934) in more details. Although I could not succeed to trace the whole course of development in both the female and male for the Japanese peculiar acrothoracican *Berndtia purpurea* UTINOMI, the following accounts concerning the young stages of the female and male and the detailed structure of the male will contribute to

1) Contributions from the Seto Marine Biological Laboratory, No. 376.

the embryological study of the Acrothoracica to some extents.

Post-embryonal Development of the Female

According to KÜHNERT (1934), *Trypetesa lampas* is sexually mature and fertilizes during the summer from May to August in Helgoland, and its larvae are, according to VISSCHER (1938), found most abundantly in June but rarely in late July and August in the water around Woods Hole, North America.

In my case, the specimens of *Berndtia purpurea* collected at intervals during the late summer period of August-September were mostly over 5 mm in total length, thus sexually mature in a condition of being more than one year old. Yet individuals containing fully developed ovarian mass and eggs were comparatively few in number, although mature males were sometimes found together with the females (See Table 2, p. 000). The rest of larger ones were found to contain only a medium-sized ovary and a few also with developing ova. A few small individuals, apparently liberated in this summer, were occasionally found on the surface of the coral inhabited by the adult females. Most of them measured about 0.8 to 1 mm in total length. The ova contained in the mantle cavity of the adult females were all in an advanced stage of development just before hatching. No or little individual which contained the developed nauplii freely in the mantle cavity was ever found.

Previous authors state that the metamorphosis of *Trypetesa lampas* from the egg to the metanauplius hastily takes place within the mantle cavity of the parent, and that the free-swimming cypris larva is then removed from the parent. From the condition of the gonad and larvae mentioned above, it seems certain that the fertilization of *Berndtia purpurea* actually takes place and the succeeding development advances very rapidly during the early summer, as in *Trypetesa lampas*.

The early development of the eggs generally agrees with that of *Trypetesa* described by HANCOCK (1849). The number of eggs carried by an individual is generally from 20 to 60, but may be as large as 90 (*cf.* Table 2). This number coincides well with that in the case of *Cryptophialus minutus*, which is according to DARWIN (1854) only 19 to about 60, the number being less numerous than in the deepsea-living Scalpelliform cirripeds and further exceedingly less than in most of the littoral cirripeds.

The development of the fertilized eggs proceeds in the mantle cavity of the parent. The eggs are all connected together by a delicate transparent membrane investing them to form the so-called ovigerous lamella. The developing ova here examined all belong to the last blastula stage or more advanced embryo, so that I have failed to observe the whole course of segmentation. However, in all probability, the segmentation of the ova may advance essentially in the same

way as in ordinary cirripeds, as known through the works by GROOM (1894) and BIGELOW (1902) on *Lepas* and by KRÜGER (1922) on *Scalpellum* and by DELSMAN (1917) on *Balanus*.

The youngest stage of segmented ova observed tolerably well is shown in Fig. 1B. They and more advanced ones are ellipsoidal in shape and enveloped by an extremely thin membrane (*e.m*) leaving a slight space between. They measure about 0.26–0.33 mm in longest diameter and about 0.22–0.24 mm in shortest diameter, which size varies little in individuals and not much more than in the

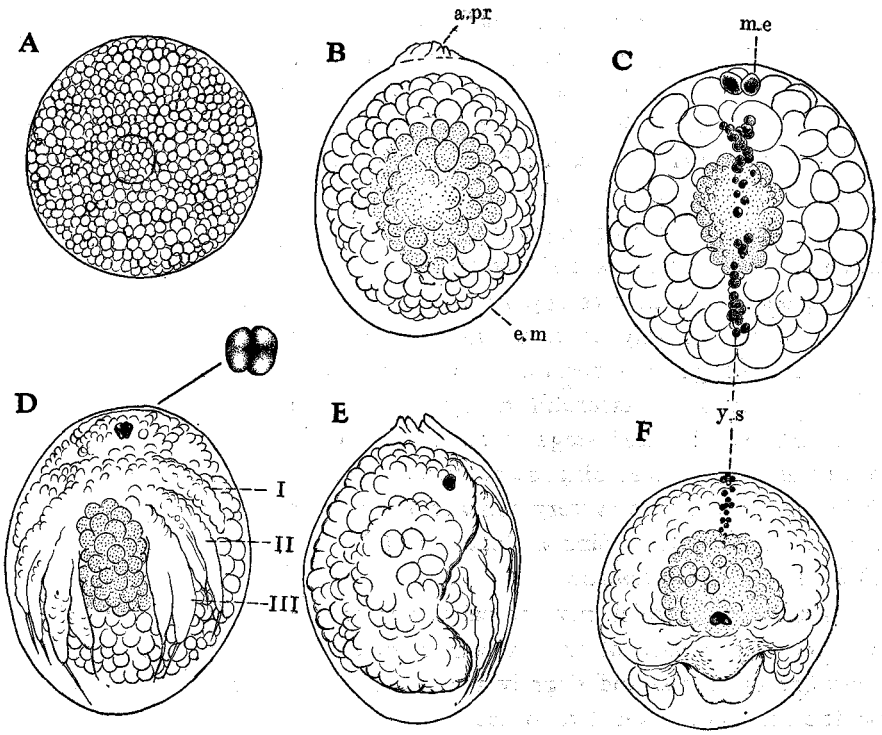

Fig. 1. Post-embryonal development of the female of *Berndtia purpurea* UTINOMI. A, unfertilized ripe egg. B, youngest embryo in egg membrane. C, more advanced embryo showing the median eye appeared in front, dorsal view. D, nauplius-egg with three-paired appendges (I–III), ventral view. E, the same, lateral view. F, the same, frontal view. Lettering as on p. 446. [×120]

unsegmented ova whilst within the oviduct. Usually one pole of the egg membrane is constricted to form a slight attachment-process (*a.pr*) by which the egg connects with the adjoining one.

The embryo, in which the segmentation has been totally completed, is colored maple orange in its central part and surrounded with the homogeneous spherical cell-masses (blastomeres), being distributed uniformly around it. In the next stage

(Fig. 1C), the central part becomes smaller than before and aggregated to an orange-colored distinct cluster. The remaining part becomes more slightly colored and even transparent. Along the median dorsal line of the longitudinal axis a series of lemon-yellow substances (*y.s*) begins to appear over the surface, but not on the ventral side. Such yellow substances do not appear in the course of segmentation of other ordinary cirripeds, as far as I am aware. In this stage, appears the first rudiment of the median eye (*m.e*), lying at the upper end of the median row of yellow substances, despite that the actual differentiation of limbs does not yet take place. This fact seems to be an important peculiarity in development, common to all members of the Acrothoracica. The formation of a median row of yellow substances, by which the dorso-ventrality of the egg is clearly perceptible, may also be characteristic. The rudiment of the median eye, lying somewhat towards the ventral side, is purplish black and distinctly divided into two symmetrical lobes which are united together in the middle. Its structure differs little from that of the nauplian eye in ordinary cirripeds (FALES, 1928).

As to the succeeding segmentation of the embryo in ordinary cirripeds, earlier authors such as BIGELOW and DELSMAN have arrived at the same conclusion that two segmentation furrows appear first on the dorsal side, instead of ventral, and become deeper rapidly to form the three pairs of appendages, and that as soon as the appendages are formed, their attachment proceeds to the ventral side. However, I could not ascertain the above fact in this acrothoracican. As is shown in the shortly advanced stage (Fig. 1D–F), the dorsal side is still evenly much convex as in the preceding stage without any indication of transverse furrows, while the ventral side is very concave in the middle there, appearing the three pairs of appendages. Similar feature has already been observed by HANCOCK (1849) in *Trpyetesa lampas*.

In this stage, which may be called the egg-nauplius, the embryo is about as large as that in any of the preceding stages. Now the posterior end becomes somewhat protruded and slightly incurved. The anterior end is evenly rounded and the rudiment of the fronto-lateral horns is scarcely defined. The median eye is bilobed, with a distinct median incision; each lobe is more elongate than before and often marked with a slight transverse constriction dividing into two parts each of which represents a visual cell. On the ventral side appear the three pairs of appendages; of these the first one is still simple, while the remaining two are biramous and each ramus is provided with a short bristle at the end.

As development still goes on, the segmentation of the appendages becomes distinct and the number of bristles on the appendages increases. The peculiar yellow substances on the dorsal side disappear, probably as decomposed with yolk substance. The fronto-lateral horns become more distinct and on each side below the median eye soon appears a frontal filament. The posterior end of the body becomes more pointed and greatly elongates to develop into the thoraco-abdominal

process, though still incurved. Still the dorsal side of the body is strongly arched. Through such change, the embryo comes to present the typical features all characteristic to the nauplius larva of the Cirripedia. Now it measures about 0.32 mm in length as well as breadth, excepting the terminal process (Fig. 2A, B).

The larva of such a stage has already undergone its full development in the egg and is ready to hatch out. Such a larva is observed in stretching movements within the egg-membrane and in pressing the arched back against the membrane as if it attempts to free itself. Eventually, the membrane ruptures at its antero-dorsal region, whence emerges the larva into the exterior.

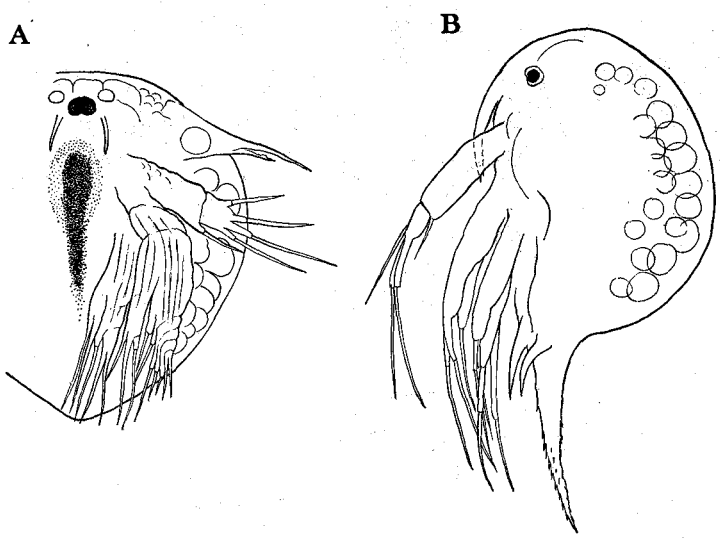

Fig. 2. Nauplius larva immediately before hatching in ventral view (A) and in lateral view (B). [×140]

Older Nauplii

The hatched larva is the same as that of *Trypetesa lampas*. Such a nauplius (Fig. 3A) measures 0.47 mm in length from the anterior end to the end of the ventral thoraco-abdominal process, and 0.26 mm in width across the dorsal shield immediately posterior to the fronto-lateral horns. The size here given corresponds to that of *Trypetesa lampas* (0.45 mm long after KÜHNERT), and is apparently about twice as large as that of the corresponding stage of ordinary cirripeds; for example, 0.22 mm long and 0.12 mm wide in *Balanus crenatus* (HERZ, 1933), and 0.24 mm long and 0.14 mm wide in *B. amphitrite albicostatus* (ISIDA & YASUGI, 1937). This interesting fact that the large-sized eggs in small number are contained in the female, is probably due to the reduction of metamorphosis resulted from its semiparasitic or hypobiotic habit.

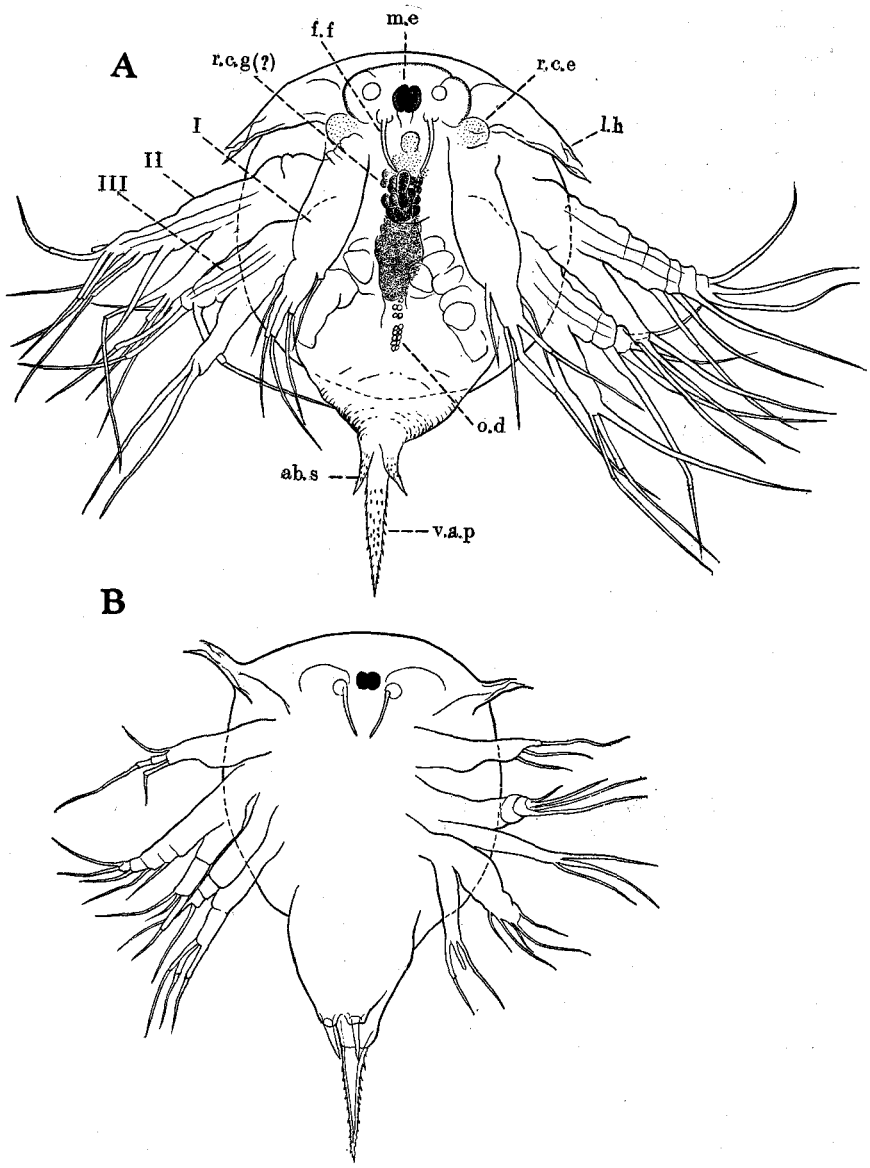

Fig. 3. A, nauplius larva just hatched out, in ventral view. I-III, first to third naupliar swimming appendages. B, nauplius larva after first moult. Lettering as on p. 446. [A ×140; B ×120]

The dorsal shield of the body is ovoid in outline, broad in width, and its posterior end is evenly rounded without any spine; thus it is more plump than that of ordinary cirripeds. The ventral thoraco-abdominal process (*v.a.p*), measuring about 0.14–0.17 mm in length, is sharply pointed at its end, instead of being forked. From its base a pair of short abdominal spines or 'Seitenstacheln' (*ab.s*) are produced backwards. Both the process and spines are wholly covered with minute spinules. The fronto-lateral horn (*l.h*) is directed posteriorly and opened at its end. The median eye (*m.e*) is formed of two symmetrical ovoid lobes fused together. Immediately posterior to the eye a pair of the frontal filaments (*f.f*) are situated, as is the case with *Trypetesa*—its situation to the eye seems to be characteristic to the nauplii of all acrothoracicans. On each side of the eye there is a large, round and vacuolated structure of empty content. The brain attached posterior to the eye is not clearly distinguishable from the outside, but the rudiment of the cypris eyes (*r.c.e*) can be seen at the base of the first swimming appendage. The central part of the mid-line of the body is nearly opaque and mounded with purplish-brown visceral mass (*r.c.g*) under the surface, which may answer to KÜHNERT's 'Klebdrüse' in *Trypetesa*. No labrum is formed there. The rest of the interior of the body is filled with large yolk-spherules of orange color, as can be easily differentiated from the connective tissue.

All three pairs of appendages, which are homologically the antennule, antenna and mandible respectively, are slightly articulated and bear long bristles at the tip and inside of the terminal portion. The so-called 'Enditen', namely bristles at the pedicel, which usually occur in the nauplii of sessile cirripeds, are wanting. More interesting is the fact that the bristles on the appendages are mostly, though not at all, formed of two joints, the distal joint being deeply intruded at its base into the basal joint. This peculiar feature is shared also by the nauplii of *Trypetesa lampas*, as has been noticed by HOEK (1909) and NILSSON-CANTELL (1921). Probably this is also an important characteristic of the nauplii of the Acrothoracica in common.

The next stage after the first moult is slightly larger than the first stage (Fig. 3B). It measures about 0.57 mm in length and 0.27 mm in width. The thoracic portion, bearing the ventral abdominal process at the tip, has greatly elongated beyond the dorsal shield, and the spinules on the process become sparse; yet the rudiment of ordinary thoracic appendages does not appear on the ventral side of the thorax. The swimming appendages show no new structures, but the terminal bristles begin to degenerate, as described by KÜHNERT in *Trypetesa*. In all other cirripeds as well as in most of other crustaceans, the bristles on the appendages usually increase their number and size rather regularly with every moult, while the present case (probably other acrothoracicans also) is quite opposed to the above. This fact suggests that the nauplius stage passes on very rapidly in the whole course of metamorphosis and does not moult so many times

Table 1. The number and length of bristles on the appendages in the nauplius stage.

Number of bristles	Unhatched nauplius	1st nauplius after hatching	2nd nauplius after 1st moult
1st appendage	5	5	3
Exopodite of 2nd appendage	7	6	5–4
Exopodite of 3rd appendage	4–3	4	4–2
Length of terminal bristle on exopodite of 2nd appendage	0.08 mm	0.19 mm	0.10 mm

as does that of ordinary cirripeds (See Table 1).

The succeeding stages of metamorphosis up to the cypris could not be followed out. According to KÜHNERT (1934), the larva of *Trypetesa lampas* developes to the cypris passing through three nauplius stages and one metanauplius stage in about a week, though VISSCHER (1938) states that it passes through six nauplius stages or moults, as is the case with most littoral cirripeds. Although little data are available, I am rather inclined to support the former view from the above-mentioned fact. However, it is out of the question in the present case whether or not it truly passes through the metanauplius stage as does *Trypetesa*. As to this problem one will be referred to the statement on the development of the male given later.

Post-larval Development and Disc-formation in the Female

The young larva of the female which has finished the metamorphosis is about 1 mm in length and 0.4 mm in width, as far as I observed. Its general feature differs in no respect from that of the adult female, except that the orifice on the rostral side lies parallel to or a little obliquely to the longitudinal axis of the animal, instead of being at right angles to the latter.

Such a larva is lodged, without exceptions, on the soft tissue of living corals lying on the crevice between the septa of calices, the rostral side with a slit-like orifice facing upwards and the carinal side downwards. The uppermost end, which agrees with the carinal end of the orifice is invariably directed toward the margin of the calice and the opposite end is deeply concealed in the soft tissue toward the central mouth, so that the animal lies obliquely to the surface of the coral. Accordingly, the rostral face below the orifice, which will develop into the attachment-disc in future, is partially exposed outsides in the early stage. However its lower end does not reach the calcareous skeleton of the coral as yet (Fig. 4). From such mode of attachment it may be assumed that the young larva first settles on the soft tissue of the coral obliquely to the surface, and then continues to grow in circumferences, before actually excavating by its own power.

At the beginning of excavation, the larva adheres, as usual in all the others, to the surface of the soft tissue of the coral with the antennules at its anterior end. As regards the position of attachment of the antennules in the young of *Trypetesa*, opinions of earlier authors are diversified. DARWIN (1854) first considers that the antennules are attached to the anterior or lower end of the mantle ('peduncle' as he calls), while BERNDT (1903a) and GENTHE (1905) maintain that they are attached near the lower end of the orifice where the body connects with the mantle. A recent study on the development made by KÜHNERT (1934) substantiates that the former view is more accurate. The same view can be applied to the present case. Namely, as clearly shown in Fig. 4, the rostral side of the mantle below the orifice is quite free from the area of attachment in the larval stage. Although I have not seen such an early stage still bearing the antennules,

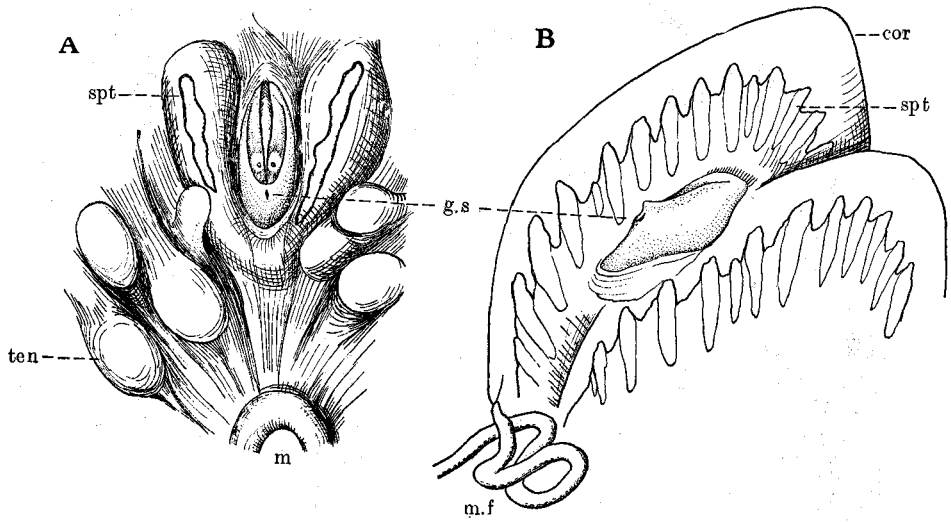

Fig. 4. Initial posture of young *Berndtia* lodged on the soft tissue of the coral *Leptastrea purpurea*, in upper view (A) and in lateral view (B). Lettering as on p. 446.

it may be admitted that when the young female is once attached, its anterior or lower end grows to extend upwards and the antennules attached there soon become wholly degenerated.

Around the lower end of the animal which is wholly embedded within the soft tissue of the coral, a thin calcareous layer is sometimes seen. This outer coat (Fig. 5A–C, *c.l*) is made up of fragile and irregular patches of calcareous matter, but not cemented to the surface of the animal. Undoubtedly this is by no means the product from the animal proper, but that from the host coral, as the secretion and deposition of calcareous substance may be induced owing to the occurrence of this intruder. With the accumulation of calcareous substance according to the gradual upward growth of the host coral, leaving alone the

surrounding part of the orifice. As the upward extension of the calice of the coral and the growth of the animal in all directions proceed on, the lower end of the animal becomes to adhere to the calcareous skeleton of the coral. Further, the cavity thus formed around the animal in the coral becomes deeper and larger by its own power of excavation.

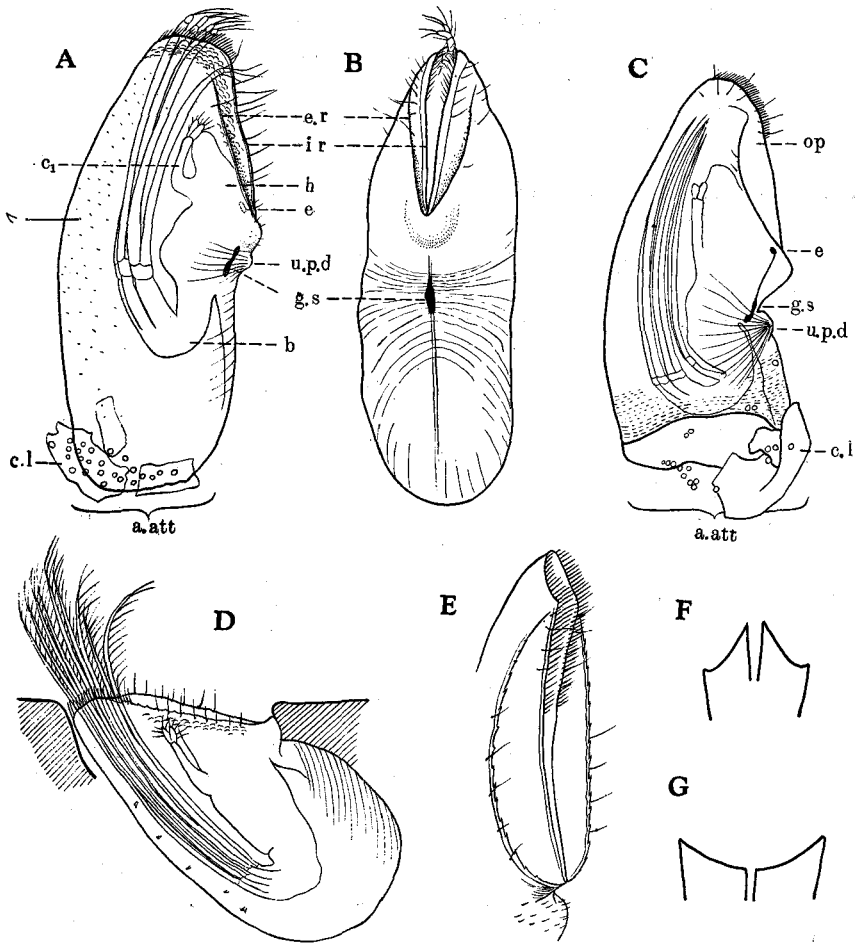

Fig. 5. Young stages of the female. A, lateral view of a specimen. B, rostral view of the same. C, lateral view of another specimen. D, a more advanced stage commenced boring action. E, frontal view of operculum in the initial stage. F, diagrammatic figure showing the section of operculum in larval stage. G, the same in adult stage. Lettering as on p. 446. [A–C ×60; D ×55; E ×80]

As growth goes on, the area of attachment around the antennules at the lower end of the animal becomes wider and longer to form the so-called disc. The external membrane over the whole surface is periodically and often moulted,

but that over the disc alone is forced to be left unmoulted owing to its adhesion to the wall of the cavity and thus becomes thicker than elsewhere, as I have noticed before (*cf.* UTINOMI, 1957, pp. 11–12; UTINOMI, 1960, pp. 257–258).

The animal is at first attached to the supporting surface almost obliquely, but later takes its position almost vertically by lengthening upward the supporting surface, as the upward growth of the coral becomes pronounced. Consequently, the disc, which was at first almost round to oval in outline, becomes narrower and more elongate like a spoon, by adding periodically the newly formed or thickened membrane above the old membranes along the rostral side at each exuviation. This is clear from the fact that the disc, when seen from inside, is

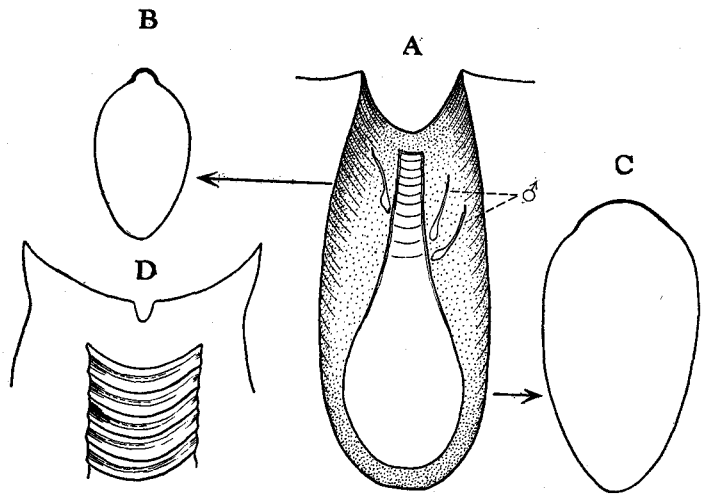

Fig. 6. A, diagrammatic figure of a longitudinal section of burrow of *Berndtia* showing the lodgement of males (♂) and the outline of attachment-disc. B, section on upper level. C, section on lower level. D. upper portion of burrow showing the cuticular laminae of disc, highly magnified.

formed of succesive laminae of cuticular structure extending beyond each other, which are defined by growth-ridges scarred on the surface, and that the laminae become distinct towards the upper end where the new zone of growth is formed; the lower rounded part of the disc, which answers to the initial position of attachment, presents no trace of lengthwise accumulation of the chitinous lammellae. A series of growth-ridges may thus record the number of times of moult (Fig. 6). Such a mode of formation reminds one much of the formation of the sublateral style as well as the attachment-disc in the rock-boring cirriped *Lithotrya* (CANNON, 1935); in the latter case, however, the new zones of calcareous laminae and cuticular coverings are, on the contrary, added on the lower margin of the

plates, as the capitular plates as well as the peduncle grow downwards at each ecdysis.

Anyhow, the formation and enlargement of the burrow is actually correlated with the growth of the host coral, so that the deepening of the burrow in this case is comparatively little appreciable. In this respect, the mode of excavation is not the same as that shown in other acrothoracicans like *Trypetesa lampas*, and also in *Lithotrya* of ordinary cirripeds. Such disparity may be due to that the latter two bore into any lifeless thing of calcareous matter, but not into living thing. As a matter of fact, the amount of excavation is more pronounced in *Trypetesa* as well as *Lithotrya* than in *Berndtia*, because of the remarkable downward, instead of upward, extension of the attachment-disc.

As the coral grows upwards, the animal imbedded within it lengthens the lower part, then the area of attachment, becomes lengthened up to the slight swelling below the orifice. Finally the animal becomes firmly cemented to the calcareous skeleton of the coral at the area of attachment in accordance with the growth of corallites. At this time the actual course of excavation first commences. The excavation is clearly mechanical, being performed by means of the chitinous spines all over the surface which were described already in detail (*cf.* UTINOMI, 1957, pp. 10–11 and fig. 5). At each excavation or contraction of the mantle, the lateral bar lying alongside the upper part of the disc may serve as fulcrum by pressing against the side wall of the burrow. This may be inferred from the fact that deposits of fine calcareous granules which may have been triturated at each excavation can be seen along the outer margin of the bar. The orifice of the burrow is usually surrounded by similar deposits of coaser granules. Such a structure is not yet formed in any early stage, before the external membrane of the mantle becomes thicker to form the cuticular coverings.—In short, the young *Berndtia* first cannot bore itself into the coral skeleton till the mantle becomes wholly surrounded by the soft tissue of the coral and then by the calcareous skeleton. In other words, after the formation of its own cavity and attachment-disc, the excavation actually takes place.

Next, I may mention the remarkable change in the remaining structures during the course of development. As stated above, the orifice in the initial stage lies in a line with the rostral surface of the mantle below the orifice, and evenly arched. The lower end of the orifice is now slightly produced. The orifice is bordered by the outer slight ridges, leaving a broad flat interspace between. The outer ridge, which arises from the lowest swelling of the orifice and blindly ends upwards, is much lower than the inner ridge forming the entire edge of the orifice; in the adult, however, it becomes more sharp and higher than the inner edge, forming the outer edge of the operculum (Fig. 5F, G). The outside of the orifice is adorned with long hairs rather sparsely all along, while the inside is furnished with a row of shorter hairs towards the upper half.

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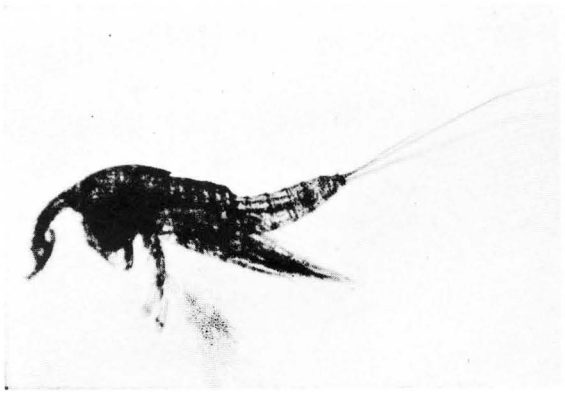
K. MATUTANI: HEAT RESISTANCE OF *TIGRIOPUS JAPONICUS*



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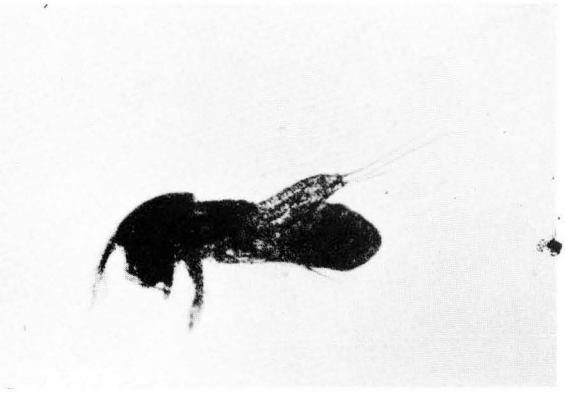

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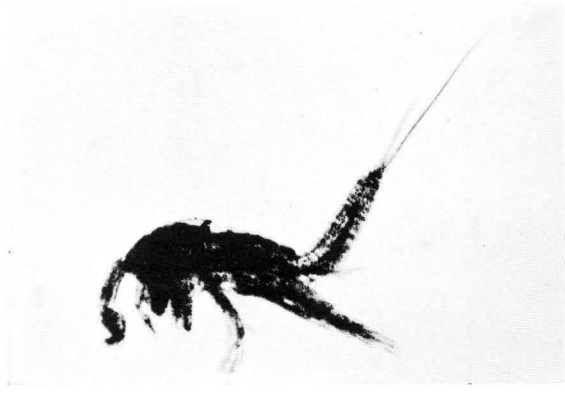

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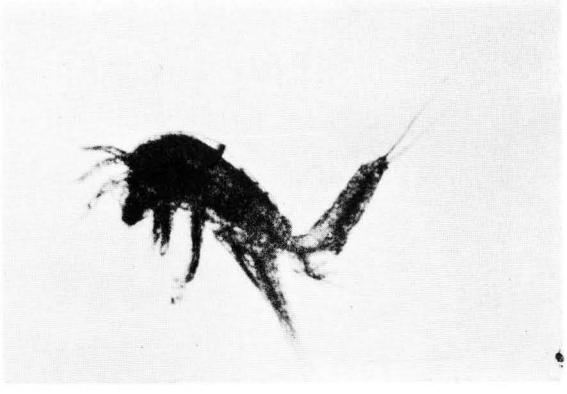

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K. MATUTANI: HEAT RESISTANCE OF *TIGRIOPUS JAPONICUS*

This inner row of hairs is the future comb-collar (Fig. 5A–E).

A little below the lower protruded end of the orifice, there is formed a slight swelling (*u.p.d*) under which an elongate black body (*g.s*) is situated. At first sight this black body appears to be a vestige of the nauplian eye, but judging from its position it may be the rudiment of the cerebral or supra-oesophageal ganglion, which is still unpaired as shown now. The true eye, which has been differentiated from the cerebral ganglion, may be seen at the same position as mentioned in the adult, though still very obscure in early stages (*cf.* UTINOMI, 1957, p. 7, fig. 2; UTINOMI, 1960, pp. 250–253). The other ganglia which are prominent in the adult are not discernible as yet.

The internal body within the sac is almost the same as in the adult, though still much smaller. The muscles of the mantle are not well developed, only with indications of radial or oblique muscle fibres running from the slight swelling below the orifice in a fan-like manner. No trace of the longitudinal muscles is discernible. This may offer another evidence for the inability of excavation by its own power still now.

Life-habit of the Male

The dwarf male of *Berndtia purpurea* can easily be obtained by searching carefully among the slit-like burrows of the female. The males are generally attached alongside the upper narrow portion of the attachment-disc of the female adhering to the wall of the burrow. They adhere by means of the terminal segment of their antennules at the anterior end to the wall of the burrow, and exclusively stand upright, extending upwards their greatly prolonged posterior portion (Fig. 6A). In some cases, however, they are exceptionally attached to the female body, lying alongside the disc. Thus, the manner of occurrence of the males in this species is quite unique among the group, for in other acrothoracicans the males are generally attached to the female body.

In each burrow of the females, 1 to 6 males are found. I have sometimes seen more than one male on the left side, but fewer or none on the right side. However, this is probably merely accidental. In this connection I examined a number of females to detect a certain relationship between the impregnation of the ova in the female and the occurrence of the males in the same burrow. Materials for this purpose are all those embedded in *Leptastrea purpurea* collected in the middle of August, 1942. A series of specimens were chosen, covering the full range of sizes of the female, and the size of each female together with the number of the males which were found together within the same burrow, were measured, and then the mass of fertilized ova contained in the mantle cavity of the female was counted. The results obtained are given in Table 2.

Table 2. Relation between the number of males and the size and development of the females.

Length of operculum of females (mm)	Number of males	Number of ripe eggs or nauplii	Condition of female gonads
1.2	1	——	——
1.7	0	——	——
1.7	1	——	——
1.7	1	14	——
1.8	0	——	——
1.8	1	——	——
1.8	1	——	——
1.8	2	+	not ripe
1.9	1	——	——
2.0	0	——	——
2.0	2	——	——
2.1	0	——	——
2.1	1	——	——
2.1	2	——	very ripe
2.2	1	——	——
2.2	1	——	——
2.2	2	——	ripe
2.2	1	65	——
2.3	0	——	——
2.3	1	——	——
2.3	2	——	——
2.3	4	——	——
2.4	1	——	——
2.4	2	——	——
2.4	2	——	——
2.4	3	——	——
2.4	3	21	——
2.5	2	——	——
2.5	1	85	——
2.6	1	——	——
2.6	3	——	ripe
2.6	3	——	very ripe
2.6	1	64	——
2.6	2	57	——
2.7	1	——	——
2.7	1	——	——
2.7	2	——	——
2.7	1	——	very ripe
2.7	1	+	not ripe
2.7	3	——	very ripe
2.7	5	+	——
2.7	5	32	——
2.8	1	——	very ripe
2.8	2	——	——
2.8	3	——	very ripe
2.8	4	——	——
3.3	6	——	very ripe

+ present, but not counted. —— absent, or not examined.

From this results, however, I could not detect any positive evidence proving cross fertilization in the same cavity, since the majority of the females are always found associated with one or more males, and some of them contain a mass of ripe ova or nauplii but none the rest. No female individual, which is not associated with the male, containing the developing ova in the mantle cavity is ever found. The number of males found to live together with one female is more in older females than in younger ones. The frequency of occurrence of sexes is on an average 1.8 : 1 between the male and female. This ratio is somewhat smaller than that in *Trypetesa lampas* (about 2.4 : 1 after KÜHNERT). This fact is very interesting when compared with the case of deepsea-living Scalpellid cirripeds having dwarf males, in which the male is much less in number than the female.

Concerning this problem, DARWIN (1854) states for *Trypetesa* that "It is obvious that these males must be very short-lived: they perform their masculine functions and then perish. We have seen, however, that after the act of metamorphosis they do grow a little, and I have reason to suspect that this is effected, as with other cirripedes, by moulting." and further says that "The females must breed more than once during their lives; and therefore successive sets of males, as in the genus *Scalpellum*, must become attached to them."

Apparently the case of *Berndtia purpurea* is also the same as the above, but as mentioned above the male is never effected by moulting of the female, because it usually does not adhere to the female. However, I met with only once the remains of an old male firmly attached by the antennules to the wall, being devoid of any internal body content. Indeed, judging from the degenerated structure of the internal organs excepting the generative organ, it is likely that the act of masculine function is a main or only object of life for himself. And from their protected habit it may be assumed that the males can survive only in association with the female, and that the ordinary cross fertilization between sexes within the same burrow may be possible.

Post-larval Development of the Male

According to KÜHNERT (1934), the cypris larva of *Trypetesa lampas* cannot be phaenotypically determined into sexes, both anatomically and histologically, until settling on any substratum takes place. Such cypris larvae as can be identified as the pure male are sometimes found attached to the wall of the burrow in which the adult female is lodged. After searching on many materials I happened to find some spats of the male newly settled, but unfortunately failed to find any younger staged larva. Nevertheless, the following observation on a series of these larvae presents not only some new and interesting facts regarding the metamorphosis peculiar to this form but also provides a problem

about the sexual dimorphism of the group.

Before describing the metamorphosis, we must take into account the peculiarities of the metamorphosis in the other known acrothoracicans. One of this group, *Cryptophialus minutus* alone shows a very unique manner of metamorphosis, as studied by DARWIN (1854), for it does not pass through the ordinary nauplius stage, but develops into the pupa bearing no thoracic appendages within the sac of the parent. In *Trypetesa lampas*, on the other hand, the larval development is performed by passing through three ordinary stages, such as nauplius, me-

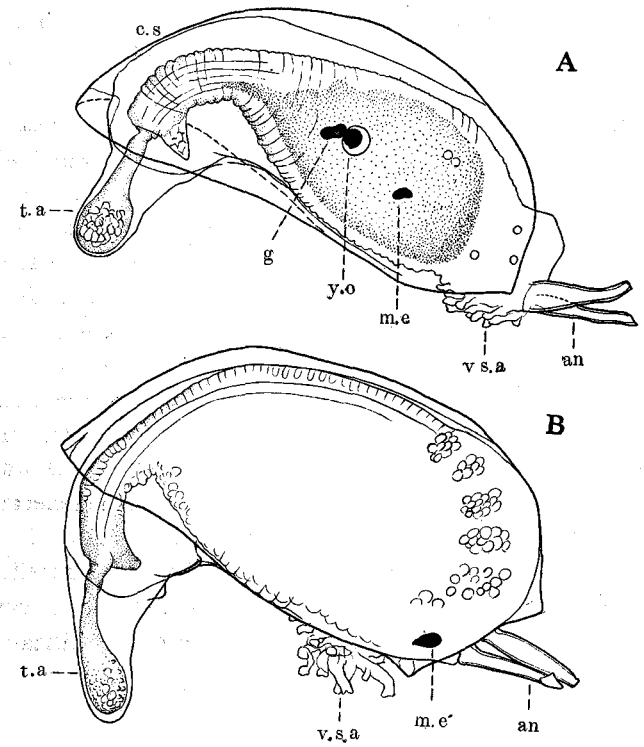

Fig. 7. Pupal-staged larvae of the male (A, B). Lettering as on p. 446. [×120]

tanauplius and cypris, as usual in other cirripeds, although it proceeds on more hastily ; in the nauplius stage, three pairs of swimming appendages are present and in the later stages six pairs of thoracic appendages also can be seen in both sexes, as in ordinary cirripeds (KÜHNERT, 1934). In this way, the larval development of *Berndtia purpurea*, at least in the male, is more like that of the former *Cryptophialus* than the latter *Trypetesa*, and probably represents about an intermediate state between them.

All the larval specimens I have examined are of the oldest pupal stage,

showing nearly the characters of the adult male. As is shown in Figs. 7 and 8, the general feature of these pupae exhibits definitely several peculiarities in comparison with the same-staged males of *Trypetesa*. In a somewhat younger form measuring about 0.5 mm in shell-length and 0.23 mm in breadth, the main part of the body is completely enclosed within the bivalve shell (cypris-sac) which has developed from the dorsal shield of the nauplius larva. The cypris-sac (*c.s*) is almost the same as that of any other cypris larva, except only that its anterior end is somewhat pointed.

The body under the shell is flask-shaped, though not so elongated as in the adult male, and encircled all over with numerous transverse wrinkles and completely enclosed within the closed mantle-sac in a constricted state. At the anterior end of the ventral surface, a pair of simple rod-like antennules are protruded anteriorly: it consists of apparently one or two segments, as in the adult. On the ventral surface near the antennules there remains an entangled mass of chitin exuviae (*v.s.a*); from its position they may be referable to the vesitiges of the second and third swimming appendages (antennae and mandibles) appeared in the nauplius stage. This fact is of great interest and presents a striking contrast with the fact that in other cirripeds such naupliar appendages are always reduced to shapeless vestiges in the metanauplius stage and then completely thrown off before passing into the cypris stage. Indeed, the cypris larva of *Trypetesa* has the thoracic appendages still remained but not the naupliar swimming appendages. In the present larva, however, the thoracic appendages are quite lacking, as is the case with *Cryptophialus*.

In ordinary case, the thoracic appendages appearing on the posterior thoracic region at the metanauplius stages are contained within the mantle cavity which is open to the exterior through the mantle opening as in the adult. In the present form, however, the body contained under the cypris-sac is completely enclosed within the mantle sac, which is composed of a continuous thin transparent membrane without any opening. This membrane is possibly the remnant of the body wall at the nauplius stage, since the body proper becomes once reduced in size to form the construction of the adult stage by moulting. Attached to the posterior end of the body, there is a remarkable terminal ampulla (*t.a*) which is already well developed as large as in the adult; it measures about 0.14 mm long and 0.05 mm wide. It is much protruded by far beyond the ventral margin of the cypris-sac, but still wholly enclosed by the membrane of the body mentioned above. The terminal end of the body at the base of this ampulla is produced ventrally into a triangular lobe, which is more marked than in the adult stage. If the ordinary metanauplius stage like that of *Trypetesa* precedes this cypris stage, the vestiges of thoracic appendages should still remain within the closed mantle-sac. Yet there remains no vestige within it, despite that the naupliar appendages still remain on the anterior portion, as mentioned above. This fact

may lead us to a supposition that the present form does not pass through the ordinary metanauplius stage in its developmental cycle.

The internal structure of the body is not clearly differentiated as yet, because it is filled compactly with the opaque, pulpy granular matter. But three peculiar black spots can be easily defined. Of these the posterior two are always closely attached; of which the anterior one is larger, rounded in outline and colored more lightly than the posterior one. These two spots are undoubtedly the yellow body and main nerve ganglion respectively, as will be stated below for the adult. The remaining one, which is widely separated from the above two, is wholly black and oval to irregularly round in outline; this is probably the vestige of the median eye in the naupius stage (*m.e'*). Such a black spot is never met with in the adult male. Moreover there is no direct communication between the nauplius-eye and the main nerve ganglion. In regard to the male pupa of *Trypetesa*, KÜHNERT (1934) states that "Bauchmark und Gehirn mit aufsitzendem Nauplius-Auge wachsen aufeinander zu, um dann zu dem definitiven und ein-

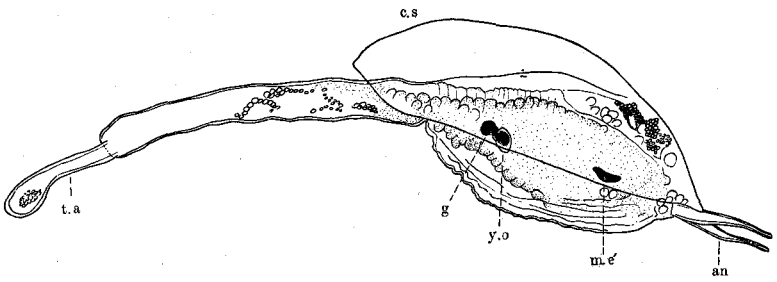

Fig. 8. Young stage of the male with a cypris-sac wholly remained.
Lettering as on p. 446. [×90]

zigen Ganglion des jungen Mänchens zu verschmelzen. Das unpaare Nauplius-Auge bleibt erhalten." I could not distinguish any cypris-eye still remained owing to the opaqueness of the interior, but its presence is certain, as will be stated below.

In a still more advanced stage (Fig. 8), the cypris-sac still perfectly remains but the vestiges of naupliar swimming appendages are entirely lost. The nauplius-eye, beside the main nerve ganglion and yellow body, is also still present. However, the remaining internal organs such as the genital organ are not yet developed. The body is more elongated as the prolongation of the posterior portion proceeds; the whole length of the body, not including the terminal ampulla, is about 0.88 mm, that is, nearly the same as in the adult, and the posterior prolongation is about 0.47 mm, being longer than the anterior thoracic region.

The mantle-sac, in which the body is enclosed at the younger stage, is reduced to shapeless vestige closely beneath the cypris-sac (*c.s*) which is ready to

cast off. The ventral surface of the body is longitudinally striated or rugged. Both the antennules and terminal amplla are almost the same as in the adult.

Morphology of the Adult Male

External Appearance. The adult male (Figs. 9–12), as compared with that of the other acrothoracicans, is very unique in shape, although it resembles in many respects of the internal characters. The body when fully developed is much elongated and tadpole-shaped; its anterior portion which carries a pair of antennules at the rounded end is broad and gradually tapers towards the probosciformed posterior prolongation. At the posterior end there is a peculiar ampulla-like sac (*t.a*). Cross section through every portion shows a round shape. The whole length of the body is about 1.2–1.5 mm, while the width is about 0.2 mm in the anterior portion and about 0.05–0.06 mm in the posterior prolongation.

The anterior main portion of the body corresponds to the 'peduncle' of *Trypetesa* and the posterior prolongation to the 'capitulum' both of which are called by DARWIN and BERNDT. However, the application of such division of the body as used in the pedunculate cirripeds is inadequate, since there is no distinct demarcation between the anterior and posterior portions; the external resemblance in the case of *Trypetesa* is merely analogical.

Cypris-sac and Antennules. In most cases, the anterior portion of the body is coated with the remnant of the cypris-sac, which is the dorsal shield of cypris-larva (*c.s'*), and adheres to the wall of the burrow by means of a pair of antennules (*an*) at its extremity lying near the ventral corner. In other acrothoracicans, the cypris-sac of the male is known to have been cast off at the last moult of metamorphosis, as in the female. In *Berndtia purpurea*, however, I have not ever found such a nude male even in fully developed stages, a part of the cypris-sac remaining in contact with the anterior end around the antennules. Judging from this fact, it seems probable that the male, when once attached, does not further moult after the final metamorphosis and hence it must be short-lived. The remnant of the cypris-sac is mostly the anterior one-third of the whole, cut off somewhat obliquely just behind the cypris-eye. The sac is smooth, transparent and chitinous all over.

Inside the cypris-sac near the cutting edge I have often found the remains of compound eyes (*c.e'*) of the cypris stage, which are not attached directly to the body proper. In one specimen examined, the remains of the compound eyes appear as consisting of nine or ten transparent globules or lenses surrounded by faintly colored granules. These globules are probably the remains of corneagen cells. Pigment bodies are completely lost. Therefore it is obvious that the compound eyes are cast off with the cypris-sac at the final course of metamorphosis of the cypris into the adult.

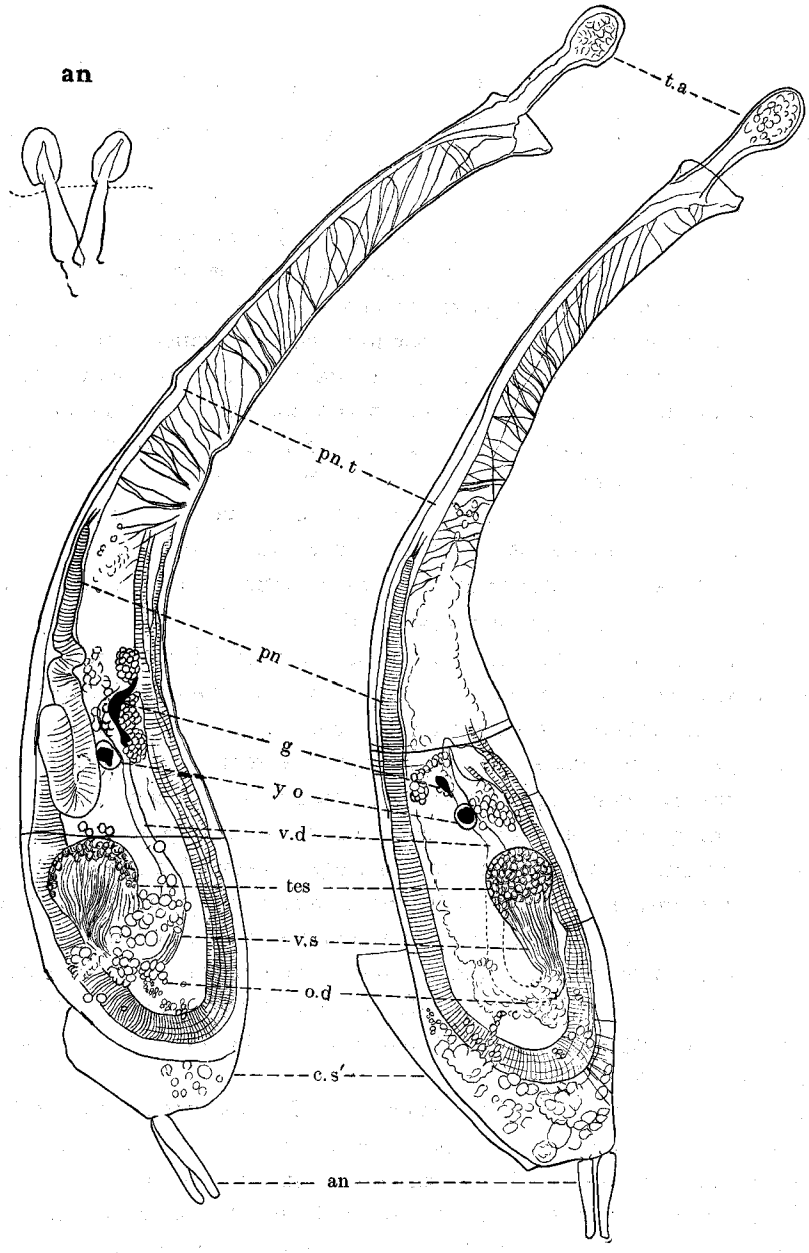

Fig. 9. The adult males with the antennules (*an*).
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The antennules (*an*), still remained in all cases, are simple, apparently consisting of a rod-like proximal segment, about 0.1–0.14 mm long. The triangular terminal segment, which I once observed, is surrounded by a transparent yellowish mass which may be considered as the product of cement or adhesive gland ('Klebdrüse'). By this terminal segment only the male is attached to the wall of the burrow. But as the wall is sticky owing to the mucous secretion of the coral tissue, the male cannot be easily detached from the wall.

Body wall and its Muscles. The whole external membrane of the body is a chitinous cuticle which is comparatively thin and transparent; hence the internal organs, even the spermatozoa, can be seen from the outsides. Cross section shows that no epithelial cell layer is formed immediately beneath the cuticle. The external surface is clothed with minute thorns (*th*) arranged in transverse intermittent rows, as in the males of *Scalpellum*-species; sometimes these thorns are massed together transversely, not quite so regularly in one row as shown in Fig. 10, and only separated from one another by many transverse folds, of which one or two are particularly distinct and completely surround the body. As a rule, these thorns are all directed posteriorly. They are evidently homologous with the chitinous spines on the mantle of the female described before. According to STEWART (1910), the sensory hairs on the males of *Scalpellum*, which are the same as these thorns, are the specialized outgrowths of the external cuticle and presumably act as the sensory organ, being supplied with peripheral nerves and sensitive to vibration of the water. But I could not detect any trace of nerve in this form.

Just beneath the external cuticle, a layer of very powerful longitudinal muscles (*l.m*) is present. But they are confined to about the middle part of the body, not extending far towards both the anterior and posterior extremities; most of them are about one-third of the whole length of the body. These muscles are bilaterally arranged, one along the dorsal surface and the other on the ventral, leaving a space on the lateral sides between them; both the ends of each muscle are somewhat expanded and attached to the external cuticle. The number of muscles is variable according to the size of the body, but in full-grown specimens about 16 on the ventral side and 19 on the dorsal side. The length is also variable, but generally they become longer and stronger towards the dorsal and ventral sides. All these muscles are, to my surprise, devoid of any trace of transverse striae; in *Cryptophialus minutus*, however, the longitudinal muscles are, according to BERNDT, distinctly striated. As a matter of fact, the body is always fully stretched and can be little contractile; hence I do not suspect that these muscles are of a ligamentous construction, giving support to the whole body. No transverse muscle or fibre is found at all. The posterior prolongation of the body lacks the muscles of any kind, though it is very elastic; possibly it is not contractile too (Figs. 10 and 12).

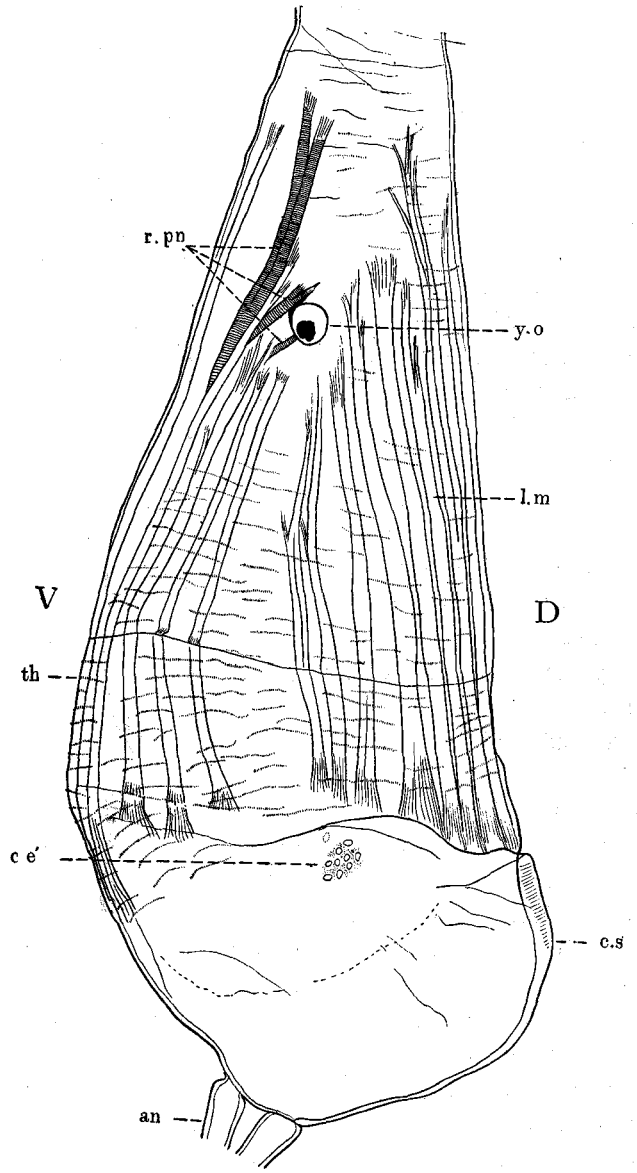

Fig. 10. Anterior portion of the male showing the external surface and longitudinal muscle layer, in lateral view. D—dorsal side, V—ventral side.
Other lettering as on p. 446. [×210]

Genital Organ. Of the internal organs of the male, the genital organ is the most conspicuous, occupying almost the whole interior of the anterior portion. The condition of the gonad included within is exclusively of a male character. And the fact is just as it had been expected, there are indeed several highly characteristic features of the male organ that have been revealed in the males of other acrothoracicans as well as some Scalpellid cirripeds.

The male organ is ordinary in structure and consists of a single continuous tube which can be divided into four sections, the testis, vesicula seminalis, vas deferens and ductus ejaculatorius; the former three are situated in the connective tissue, while the last one is wholly enclosed within the sheath of the penis. The entire tract is considerably longer than the body (on an average twice as long), and therefore has a looped or winding course, which mode is peculiar to this form.

The testis (Figs. 11 and 12, *tes*) is situated in the center of the widest anterior portion and opens anteriorly, instead of posteriorly. It is a large globular or pyriform sac, measuring about 0.07–0.09 mm in diameter, and filled with compact mass of sexual elements which arise from the epithelial lining under the tunica propria. In moderately developed males, various developmental stages of the sexual cells may be met with, the spermatogonia (*spg*) occurring in the basal part (posteriorly to the body axis) and the spermatozoon (*spz*) in the portion leading into the vesicula seminalis. The spermatogonia are generally massed together, not diving into several groups such as shown in *Trypetesa* (after BERNDT). They are generally spheroidal in shape and as large as 5μ in diameter and enclose numerous chromatic substances; the nuclei could not be distinctly differentiated.

Successive developmental stages of the sexual cells up to the spermatozoon could not be followed out, but some of smaller cells more faintly stained with dyes are inserted—this is probably the spermatid stage. The spermatozoon is filiform, having a pinhead-like or pyriform head. Its proper length is not clear as it is too fine to be traced all the way.

The actual limit of the vesicula seminalis (*v.s*) which in most cases contains mass of thread-like spermatozoons is not strictly differentiated, since it is merely represented by a slight swelling at the place where it communicates with the testicular sac through gradual tapering, no distinct constriction such as shown in other acrothoracicans occurring between them. Thus, the vesicula seminalis is nothing but a dilation of the proximal part of the vas deferens. At this place the canal turns abruptly backwards and runs for some distance straightly. This part, answering the vas deferens (*v.d*) is a simple, narrow and empty duct, measuring about 10–15μ in diameter, and a little longer than one-fourth of the whole body. Cross section (Fig. 12A) shows that the wall consists of only a very thin cuticular tunica propria which is continuous throughout the canal; no epithelial cell could be detected.

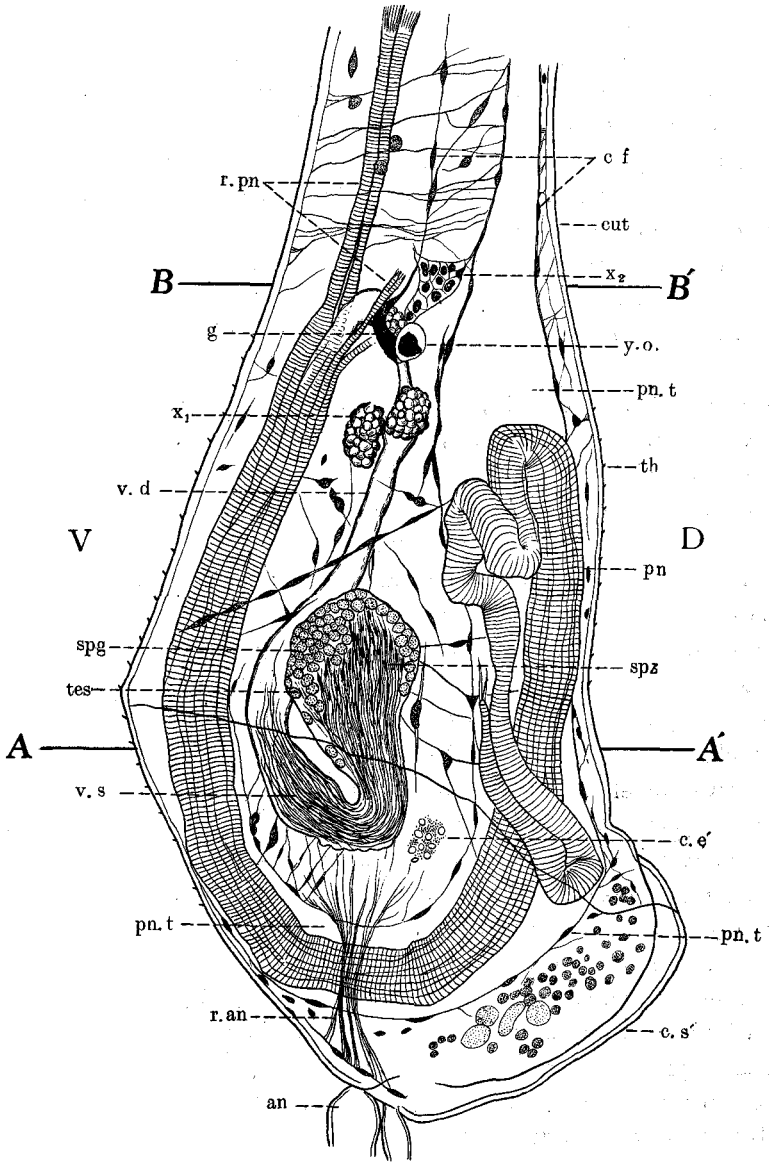

Fig. 11. Anterior portion of the male showing the internal structure, in lateral view. A–A′, B–B′ represent the cutting levels of cross sections (A, B) given in Fig. 12.
Other lettering as on p. 446. [×210]

At the end of the vas deferens, where it is particularly narrowed, the canal turns back again towards the anterior extremity, and enters into the ductus ejaculatorius (*d.ej*) forming the penis. At the base of the penis there are several bundles of powerful striated muscles adhering at the their proximal ends to the connective tissue of the body; these muscles consist of two groups, one longer running longitudinally and the other shorter running obliquely. These muscles (*r.pn*) gather round the base of the penis and enter into the penis sheath to form together an outer circular layer of longitudinal muscles (*l.m.p*). Probably their commencements may act as the retractor in aiding the long probosciformed penis

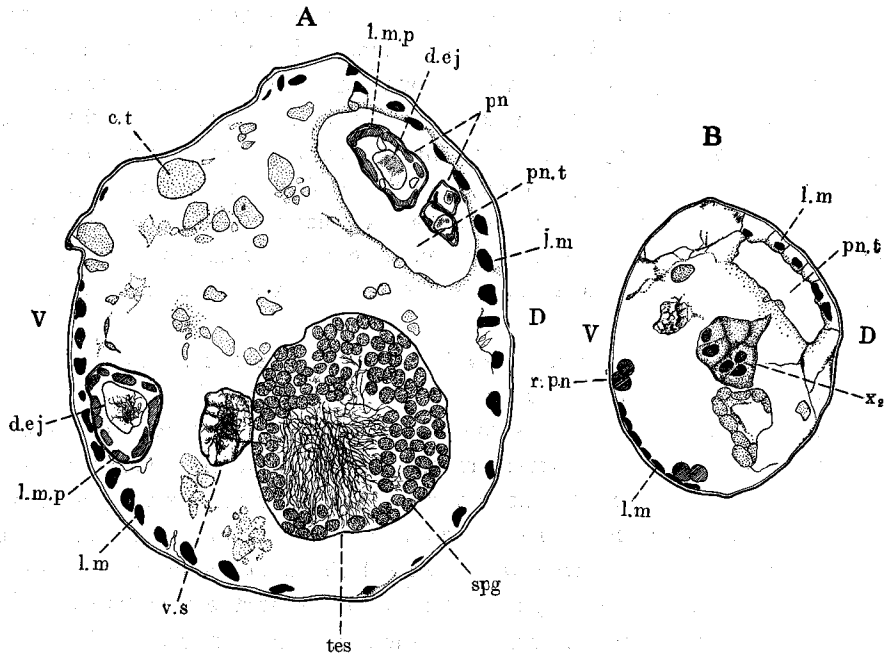

Fig. 12. A, transverse section of the anterior portion of the male, cutting along the line A–A′ shown in Fig. 11. B, transverse section of the median portion of the male, cutting along the line B–B′ shown in Fig 11.
Lettering as on p. 446. [×330]

to withdraw itself into the body cavity, *i. e.* the penis-tube by their contraction. Similar retractor muscles or fibres are present in the allied *Trypetesa* and *Cryptophialus* too.

It is quite surprizing that the structure of the penis does not conform with that of other acrothoracicans described by earlier authors. The penis (*pn*) is of a remarkable length and greatly contractile; it starts from about the middle portion of the body, and runs forwards closely along the ventral surface of the body parallel to the foregoing genital tract. When it reaches the anterior ex-

tremity of the body, it turns backwards again forming a slight coil and then runs along the dorsal surface to the terminal end of the posterior prolongation. It runs freely within the channel-like body cavity throughout the whole length, except for its proximal portion on the ventral side where it passes through the connective tissue. The penis lies, as a rule, coiled up and entangled like an intestinal parasite within the widest portion of the channel-like body cavity named the penis-tube (*pn.t*), but even if stretched out, probably it does not attain the terminal end of the penis-tube, as inferred from its total length. In moderately stretched state the penis is approximately 0.1 mm in length and 0.03 mm in average diameter.

The penis is plainly annulated all over. It tapers gradually and terminates with a brush of few fine bristles. It is furnished with finely striated longitudinal muscles (*l.m.p*) arising from its base or extending from the retractor muscles at its base. These muscles consist of about as many as 10 bundles in the proximal portion, while fewer than 5 in the terminal portion. They form together with the ringed cuticular covering an outer sheath (*pn.s*) for the penis to enclose the ductus ejaculatorius within it. The ductus ejaculatorius (*d.ej*), which is a continuation of the vas deferens, is usually convoluted and attached at its end to the outer sheath. No other muscle such as the circular one is inserted between them (Fig. 13B).

In the males of *Trypetesa* and *Cryptophialus*, on the other hand, the penis is known to be furnished with circular muscles, and according to BERNDT (1903a), the retracter muscles lying at its base become weaker towards the penis and ultimately to form merely an outer layer of finer longitudinal muscle fibres. On this point attention should be called to the presence of an outer layer of strong longitudinal muscles in the penis of most ordinary cirripeds. In the ordinary group, the circular muscles, even when present, lie inside the layer of longitudinal muscles and are formed as the outer covering of the ductus ejaculatorius proper. Consequently I suspect the presence of such real circular muscles in the penis of *Trypetesa* and *Cryptophialus*. In this connection, it is noticeable that the longitudinal muscles around the body are non-striated in *Berndtia* as mentioned above, whereas, according to BERDNT, they are finely striated in *Cryptophialus*. Anyhow, it may deserve special notice that such opposed features as to the muscular system are seen between this form and other acrothoracicans.

Nervous System. The nervous system of the male is very simple, resembling that of *Trypetesa lampas*. In the middle portion of the body where the vas deferens communicates with the ductus ejaculatorius, there is a large dark-colored ganglion (*g*), which is usually lengthened parallel to the vas deferens. This ganglion corresponds well with the 'Hauptganglion' in *Trypetesa*. In the living state, it is purely black, but when preserved in alcohol or freshwater, it becomes paler and shows a purplish yellow hue. It varies much in outline from round

to irregularly elongate (Figs. 13A and 14). In most cases, however, it appears to consist of two parts divided by a slight median constriction, of which the anterior part is almost round and the posterior one tapers distally. It is difficult to say the homology of this ganglion with that of the female, but from its shape I infer it to be fused mass of the ventral nerve ganglia. In fact, KÜHNERT (1934) recognizes from her embryological study of the male of *Trypetesa* the fact that the cerebral ganglia ('Gehirn') and ventral nerve cord ('Bauchmark') grow one after another and then become fused into a single mass at the cypris stage. Neither the optic ganglion nor the eye, which is known in the male of *Trypetesa*, is found at all, at least in the adult males. The histological structure differs

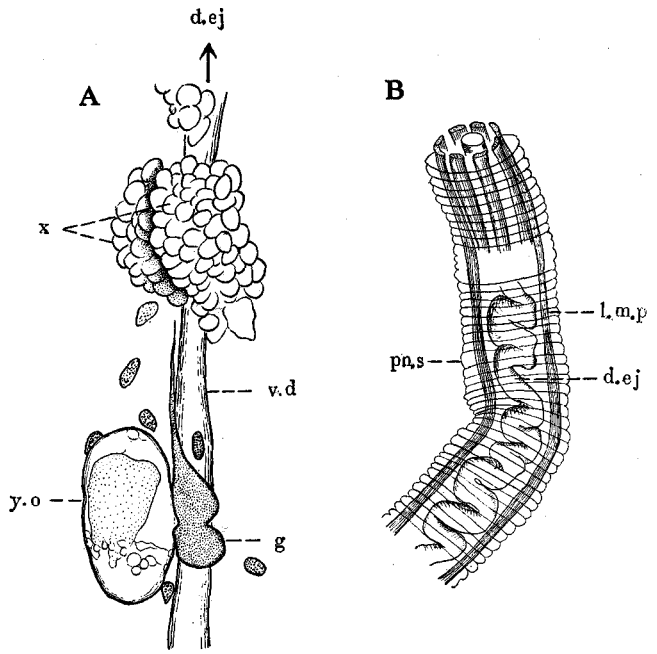

Fig. 13. A, vas deferens and its adjacent organs. B, a part of penis. Lettering as on p. 446. [×430]

little from that of any ganglion of the females which has already been described (*cf.* UTINOMI, 1960, pp. 249–253).

Visceral Organs of Indistinct Nature. In total preparations I have always met with a large yellow peculiar body lying usually in close contact with the main ganglion (Fig. 13A, *y.o*). This is undoubtedly homologous with AURIVILLIUS' 'gerundete Organ' or BERNDT's 'rätselhaften gelbes Organ' found in the male of *Trypetesa lampas*.

This yellow organ (*y.o*) is usually round, measuring about 0.03–0.04 mm in diameter, and shows an orangish yellow hue. The content itself is apparently

empty or structureless, but may be detected a thin sac-like area in the central part, not distinctly circumscribed. In the living state, the central part presents a rather dark purplish hue, so that it may mislead to be an eye or nerve ganglion, partly on account of being situated so close to the above-mentioned ganglion. However, when putting into alcohol or freshwater, the dark color becomes soon paler and even disappeared, and only remains a few yellowish granules in its marginal zone. The central part appears to be homogeneous and rather liquid-like or oily in nature, but not so fibrous as in *Trypetesa*.

As regards the nature of this organ, former authors have not given any clear interpretation. However, as suggested by AURIVILLIUS (1894), it reminds one of the 'gland of unknown nature' which has been discovered by HOEK (1884) in the male of *Scalpellum regium*. According to him, the 'gland' consists of two oval bags which are lined by an extremely delicate membrane and filled with

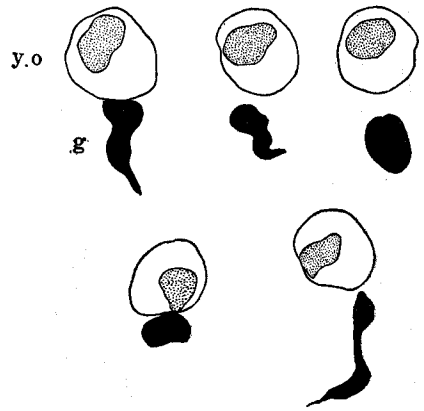

Fig. 14. Various shape of yellow organ (*y.o*) and nerve ganglion (g) of the male. [×210]

brownish yellow granular substances; he considered it to be probably the remains of the appendages of the oesophagus. In the male of *Trypetesa*, KÜHNERT (1934) observed that the rudiment of the yellow organ has first appeared at the pupal stage, being placed near the main ganglion or brain. Anyhow, this yellow organ appears to be rudimentary, as compared with the other organs. However, even if so, it is more improbable to regard it merely as functionless, judging from the fact that it occurs throughout the whole life in the vestigial male alone. It seems to me that the yellow organ is somehow a kind of nutritive organ originated from the larval alimentary canal.

In the neighbourhood of the yellow organ as well as the main ganglion, there are found the other organs or cell-assemblages of indistinct nature (Figs. 11 and 13A). They consist of, in most cases, two or three groups, or which two

(x_1) are usually situated on either side of the vas deferens and the other one (x_2) situated posteriorly near the proximal end of the penis. Each of the anterior cell-assemblages is ovoid or globular, reminding of a mulberry fruit, and measures about 0.04–0.06 mm in longest diameter. The cells are spherical in shape and evenly granular in structure, without distinct trace of nuclei, and stained intensely with carmin. The posterior cell-assemblage is, on the other hand, generally irregular in outline and formed of large cells of irregular shape, each cell containing a large round nucleus in the middle. Judging from the general outline and structure, both cell-assemblages are probably of different kinds in nature.

These cell-masses have no direct communication between them and also with the other organs or lumen in the connective tissue. Such cell-masses are not found in any other acrothoracican. On comparison with the male of ordinary cirripeds, these remind somewhat of the 'cement glands', especially found in the males of *Scalpellum velutinum* and *S. regium*, which have been described and figured by HOEK (1883, 1884). As shown in Fig. 11, the position of these cell-masses in the present male is by far separated from the anterior end of the body where the antennules are situated. Hence it is not clear whether they are the same as the ordinary 'cement glands'. However, if such a question is not taken into consideration, the position of these bodies fairly corresponds with that of the 'cement glands' in the adult males of *Scalpellum*, as well as that of the 'Klebdrüse' (larval cement gland) in the cypris larva of *Trypetesa lampas*.

In the adult males of *Scalpellum*, such as *S. scalpellum, stroemi* etc., the 'cement glands' are generally situated at the same position as in the cypris stage; that is, they lie on both sides of the vestige of stomach and two ganglia in front of the testis (KRÜGER, 1940, p. 109). In *Trypetesa lampas*, the larval cement glands ('Klebdrüse') are, according to KÜHNERT, very developed in the cypris larva, but reduced to piecemeal vestiges and finally disappear entirely during the course of metamorphosis. She further states on this point that "Ich fand nur ein Exemplar, bei dieses Klebdrüse noch völlig intakt war.—Ob diese Klebdrüse der jugendlichen Zementdrüse gleichzusetzen ist, bleibt dahingestellt. Sie erfährt im Laufe der weiteren Entwicklung eine starke Rückbildung und verschwindet bei männlichen Tieren ganz. Diese spätere Zementdrüse unterscheidet sich wesentlich von diesem Organ durch Färbarkeit, Aufbau und Kleinheit der Kerne." In highly developed cypris larva of the female after 'Klebdrüse' disappeared, she discovered the rudiment of the cement glands of the adult stage around the anterior portion of the body.

In the connective tissue at the anterior extremity which lies between the external cuticle and genital tract, I have found also abundant mass of cellular elements in the adult male of this form. They are composed of round connective tissue cells, oil-drops and remains of yolk masses, all of which are variable in size and so confusedly scattered or grouped with one another that cannot be

easily differentiated. All of them stain vigorously and uniformly with borax-carmin, rendering the examination of nuclei almost impossible. So it is very difficult to judge these cell-masses in the anterior portion as the rudiment of the cement glands of the adult stage, as KÜHNERT supposed. Nevertheless, it is not impossible to take the anterior globular bodies in question mentioned above for the vestiges of a pair of the larval cement glands. This supposition may be supported also by a comparison with the case of the Rhizocephala, in which the larval cement glands are said to be probably ultimately modified into the colleteric glands ('Kittdrüse') or reduced in the adult (FEUERBORN, 1931, 1933).

The other visceral organs, such as the digestive canal with its appendages and the excretory organs, are never found at all.

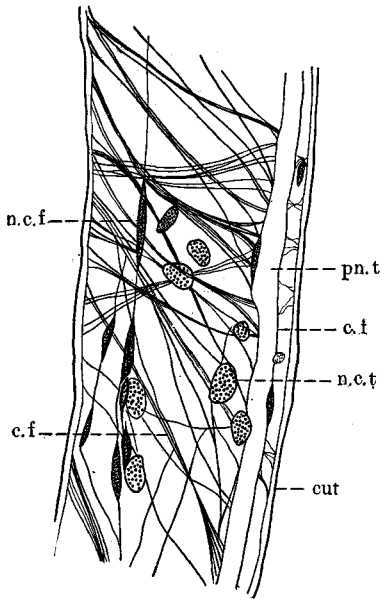

Fig. 15. A part of the posterior prolongation of the male. Lettering as on p. 446. [×410]

Connective Tissue and Penis Tube. The body is richly furnished with conspicuous connective tissue fibres forming a coarse network, and contains here and there transparent oil drops or yolk spherules abundantly. The connective tissue fibres lying in the posterior prolongation traverse obliquely and connect the penis tube (*pn.t*) lying close to the dorsal surface with the external cuticle (Figs. 9, 11 and 15). In addition, there are a few longitudinal fibres running parallel to the penis tube; they are, however, not continuous all throughout, but are formed of a number of short fibres connecting together at intervals in a single chain-like appearance (Fig. 15, *c.f*).

In the broad anterior portion, especially around the testis, the fibres are

rather entangled and run in all directions to keep the genital tract in the middle. Of these fibres those lying at the base of the antennules are particularly strong and form a bundle; undoubtedly they may act as the retractor of the antennules (Fig. 11, *r.an*).

All these fibres are provided with large spindle-shaped nuclei. Mingled with such nuclei, there are found larger nuclei of different shape, lying freely in the connective tissue. They (*n.c.t*) are depressed, round to oval in outline and measure about 13μ in longest diameter. They contain vividly stained chromatic substances but apparently lack the nucleolus. The cell outline cannot be precisely differentiated (Fig. 11 and 15).

The penis tube, which contains the penis of extraordinary length, is the broadest in the coiled anterior portion and extremely narrow in the posterior prolongation. CALMAN (1909) regards the penis tube (in *Trypetesa*) as the vestige of the mantle cavity, However, as far as my observation on this *Berndtia* is concerned, it does not agree with the mantle cavity of ordinary cirripeds, since it is never lined by any cuticle nor by the epithelial cell layer, but only surrounded by a simple layer of delicate fibres which do not differ from those in the neighboring connective tissue. Moreover, it presents no indication of invagination of the external epithelium. Hence, the penis tube is nothing but a specialized lacunar channel in the body tissue. It is not homologous with the vestigial mantle cavity found in the males of Scalpelliform cirripeds, but peculiar to the group of Acrothoracica alone.

Terminal Sac or Ampulla. There remains to be described the terminal sac or ampulla (Fig. 8, *t.a*) which I have alluded to before. It projects at the dorsal surface of the terminal end of the body where the penis opens. It is considerably developed like a flask, consisting of a long stalk portion and an ellipsoidal head portion. It measures about 0.154 mm in total length and 0.055 mm in greatest diameter, the stalk being as long as the head or a little longer. It is lined with the somewhat thick cuticular epithelium and filled with the yellowish connective tissue containing abundant nuclei, somewhat granular in apperance. The nuclei within it are round to oval, somewhat depressed in outline and connected with one another by the finely fibrous structure. However, its interior apparently does not communicate with the penis tube nor with the exterior.

Such a peculiar appendage is not found in any other male of the Acrothoracica. Structurally it does not indicate any sign of glandular nature. However, judging from its position and peculiar feature and also from being fully developed even in the younget stage, it may be a kind of the tactile proboscis serving in the act of fertilization.

Summary

1. The results of my investigations on the larval development of *Berndtia*

purpurea UTINOMI and the detailed morphology of its male are here presented.

2. The embryo of the female first grows the bilobed median eye and then becomes to show the segmentation on the ventral side. The nauplius larva is identical with that of other acrothoracicans.

3. The youngest female first cannot bore itself into the coral skeleton till the mantle becomes wholly surrounded by the soft tissue of the host coral and then by the calcareous skeleton. In other words, after the formation of its own burrow and attachment-disc, the excavation actually takes place.

4. The males are exclusively attached to the wall of the female's burrow along the female's attachment-disc, usually 1 to 6 in association with a female. Its structure is characterized markedly by the coiled course of the whole genital organ and also by the presence of a peculiar terminal ampulla at the end of the posterior prolongation. No true mantle cavity is formed.

5. The male, as well as the female, probably lacks the metanauplius stage during the whole course of metamorphosis. The thoracic appendages such as present in ordinary cirripeds are not formed altogether during the metamorphosis.

6. The vestiges of naupliar swimming appendages still remain in the cypris stage, but are ultimately thrown off.

7. Both the nauplius- and cypris-eyes appear during the whole course of metamorphosis, but ultimately cast off with the cypris-sac.

8. The cypris-sac usually remains partially around the antennules even in the adult stage.

9. Neither the true mantle cavity nor the mantle-like covering is formed in the larval stages as in the adult. The male body is enclosed within a thin transparent membrane beneath the cypris-sac in the cypris stage, the membrane being closed and merely a remnant of the external cuticular covering of the thorax proper.

10. In short, the larval development of the female somewhat resembles that of *Trypetesa*, while the larval development of the male shows a closer resemblance to that of *Cryptophialus*.

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LIST OF ABBREVIATIONS USED IN THE FIGURES IN THE TEXT

a.att	Area of attachment.
a.pr	Attachment-process.
ab.s	Abdominal spine.
an	Antennule.
b	Body.
c_1	Cirrus I.
c.e'	Vestige of cypris-eye.
c.f	Connective tissue fibre.
c.l	Calcareous lamellae of coral.
c.s	Cypris-sac or -shell.
c.s'	Vestige of cypris-sac.
c.t	Connective tissue.
cor	Corium of coral.
cut	Cuticle.
D	Dorsal side.
d.ej	Ductus ejaculatorius.
e	Eye.
e.m	Egg membrane.
e.r	External ridge of operculum.
f.f	Frontal filament.
g	Main ganglion.
g.s	Supra-oesophageal ganglion.
h	Head.
i.r	Internal ridge of operculum.
l.h	Fronto-lateral horn.
l.m	Longitudinal muscle of mantle.
l.m.p	Longitudinal muscle of penis.
m	Mouth.
m.e	Median eye.
m.e'	Vestige of median eye.
m.f	Mesenterial filament.
n.c.t	Free nucleus in connective tissue.
o.d	Oil drop.
op	Operculum.
pn	Penis.
pn.s	Penis sheath.
pn.t	Penis tube.
r.an	Retractor of antennule.
r.c.e	Rudiment of cypris-eye.
r.c.g	Rudiment of larval cement gland.
r.pn	Retractor penis.
spg	Spermatogonia.
spt	Septum of coral.
spz	Spermatozoon.
t.a	Terminal ampulla.
ten	Tentacle of coral.
tes	Testis.
th	Thorn.
u.p.d	Upper projection of attachment-disc.
V	Ventral side.
v.a.p	Ventral thoraco-abdominal process.
v.d	Vas deferens.
vs	Vesicula seminalis.
v.s.a	Vestiges of naupliar swimming appendages.
x_1	Anterior enigmatic cell-assemblage.
x_2	Posterior enigmatic cell-assemblage.
y.o	Yellow organ.
y.s	Yellow substances.